Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

ON PHYLOGENETIC CLASSIFICATION.[1]

BY THOMAS H. MONTGOMERY, JR.

INTRODUCTION.

The great diversity in plans of classification is, in part, the result of the diversity of standpoints held by their framers. Whether the observer is conscientious in endeavoring to represent the facts as they are, or whether he with more elastic conscience disregards all which do not coincide with his preconceived standpoint, the consequence is a bewildering confusion of individual, wholly subjective interpretations. While one relies upon embryological data to great extent, another trusts to the evidence of comparative anatomy, and a third unites a combination of these two methods in such a manner as he sees fit. All unite in holding similarity in structure to represent phyletic affinity, but they depart from one another on the question as to what constitutes similarity. And again, among the comparative anatomists, some attribute more value to this organ or organ system, others to that, and while some contend that similarities may be determined by the study of one particular conservative character, others argue that no character should be neglected. And he who finds only likenesses is to be ranked little or no better than he who sees only differences.

As one scheme of classification follows upon another, and in its return receives emendation and perhaps subsequent lack of support, we may well inquire whether, after all, phyletic classification may ever be earnestly considered as more than speculation. Yet those who maintain this view forget that classification is interpretation, and that interpretation here is as allowable as in any other series of facts. Classification is a grouping of concepts necessary for the mind to make, in order to secure a foothold among the enormous mass of facts of structure which no one man can grasp. And the reason for the diversity of the interpretations is the enormous number of the organisms themselves; the greater the array, the more difficult the explanation. Lamarck pointed out that no groups existed in Nature but only individuals, yet he arrayed these individuals into certain mental groupings, such as was necessary for an understanding of them.

---

[1] From the Zoological Laboratory of the University of Pennsylvania.

Classification, orderly arrangement, is demanded, so that the field of facts may be better surveyed from the vantage points thus gained. But a purely arbitrary and artificial classification, such as many museum curators of an earlier time invented in order to arrange an animal according to superficial examination alone—and such as is still used by many who would avoid patient toil of thorough examination of all the parts—is not a help to the mind, for it does not represent the organisms in their natural relationships, and hence it and the morphology must be memorized separately. Phyletic classification should be an epitome of our knowledge of the genetic relations of organisms, and many tireless workers are striving to make it so. Insomuch it may be regarded as the statement of our knowledge of the succession of evolution, and consequently, therefore, one of the main aims of zoological research. It is not only a naming and arranging of the individuals we study, not only a subservient preliminary to such study, but in its perfected condition a statement of all we have learned about the organisms. All careful, accurate observation of structure and function, and of the ecological phenomena which help to explain these, must eventually be considered in such classification, by a gradual and critical synthesis of all these facts.

All that we learn is expressed in its relations, and we define one organism in terms of another. Thus there arises a whole connected representation of the data, and whether we walk by the anatomical, the embryological, the physiological or the ecological path, all must use the same method to test their conclusions, namely, comparison. The classification that we strive for is based upon comparison, and is to represent the path of evolution as far as the facts allow us to determine it.

There has been shown by a more modern school of investigators a spirit of disapprobation if not of disgust against the plotting of "genealogical trees." To some extent they are justified in this disapproval, when we note the variety of opinions as to the relationships of many groups of animals. Thus, how few are the groups which have not been called upon to serve as the ancestors of the Vertebrates! Any one can recall the manifold opinions as to the affinities of the Rotifera, of *Macrobiotus* and the Gordii, of the Diplopode Myriopoda, of *Limulus*, of the Pycnogonida, and of *Sagitta* and *Pentastomum;* indeed, these examples could be much increased, and we could say that only in regard to very few groups is there any unanimity of opinion. Yet the phylogenist may well, in his turn, note the lack of unanimity in the conclusions reached in other lines of investigation. Has the cause of variation been explained, or have the phenomena of cleavage and differentiation, or those of cell division and inheritance, and how much is known of the interaction of sense organ and central nervous system ? The phylogenist does not answer his critics in a vindictive spirit, but to show that he as well as they must reach correct interpretations slowly. A view disproved is, after all, something gained, for it serves to narrow the field. The phylogenetic classification of animals is perhaps the greatest task that a naturalist has before him, the aim to represent the sequence and relations of all known organisms, which presupposes a thorough knowledge of their structure and an understanding of the phenomena of growth and change.

Whether such a perfect classification can ever be obtained or not, it is the part of the naturalist to aid in its pursuance, even if not by working upon it directly. One does not stop before a task for fear he cannot complete it. When one looks upon it not only as a determination of relationships, but also as involving an understanding of growth phenomena, it is found to be a project demanding the highest mental effort.

It seems that perhaps more logical and true ideas of the relationships of animals may be gained by a critical consideration of the standpoints employed—of attempting to eliminate those that may be erroneous. If the standpoints can be logically lessened, the amount of the present confusion would be reduced. The animals now living do not represent more than a fragment of the forms that have once existed, and very few of the latter have been preserved geologically. For the vast number of forms, most of those of softer structure, no paleontological remains can be expected; and therefore for the determination of the ancestry of those now existent we must rely upon the study of the anatomy of the latter. This may be the anatomy of the adult stage or of the earlier stages;

and the present contribution is in the main a discussion of the values of the comparative anatomical and of the embryological methods in the determination of phylogeny.

The materials that the phylogenist has before him are, first, the animals themselves; and second, the accumulation of previous studies upon their morphology. If the latter were always accurate representations, they would give one, in a short space of time and with a minimum of labor, the facts he needs; but very few of the large array of morphological monographs are even tolerably accurate, and because of this one frequently goes astray in trusting to the descriptions of others. Hence, first and foremost, our ideas of morphological details must be accurate—*i. e.*, without preconceived bias of interpretation—and, as far as possible, we should ourselves study the organisms which we compare. In the next place the whole method must be synthetic, comparing object with object until gradually a connected mental superstructure is formed, all the parts of which have been separately studied. This by no means implies the avoidance of working theories, for it has been the experience of the naturalist that such theories are exceedingly fruitful in directing research; but it does imply that the working theory should be considered as such and as nothing more, until it can be demonstrated that there are no overlooked facts which may be in contradiction to it. At every point the method should be tested as well as the observation. By adding comparison to comparison, provided we are working with a method in whose relative correctness we can feel confidence, we may expect fuller unanimity of result and gradual lessening of confusion in interpretation.

I. The Possible Modes of Classification.

A classification is necessary to enable a concise grouping of the facts; a phylogenetic classification should be the statement of the origin and transformation of organisms. Obviously there is a necessity of considering whether the study of structure alone is sufficient for determining this racial progress, or whether the other attributes of organisms should be considered. In a word, why should the strictly morphological classification, the one dominant in present thought, be granted precedence ?

Any of the following classifications might be instituted, besides the morphological: (1) *Physiological,* one based upon the degree, kind, and mode of interaction of those activities of parts known as functions. Here would presumably be found a progress from the more generalized to the more specialized, accompanying the evolution of the organism, just as in structural relations. (2) *Physical* or *Dynamical,* one based upon the so-called physical energies or motions; for such motions might be found to show successive complexity, according to changes within the organism. (3) *Chemical,* for increasing complexity and instability of the substances composing the organism might go on parallel with the course of racial development. (4) *Ecological,* based upon the relations of the organism to its environment, its kinds of habits and their modifications, its geographical distribution, its general responses to environmental stimuli. (5) *Psychical,* dealing with its mental operations (this might be classed with the physiological).

Now these possible kinds of classification fall into two groups, the physical and chemical, and the morphological, physiological, ecological and psychical; for while the physical phenomena of an organism may be considered by themselves, and the chemical equally so, all the other kinds of phenomena are closely correlated. We might term the physical and chemical aspects *inorganic,* and the others *organic,* were these expressions not now becoming somewhat obsolete. There may have been an evolution of the "inorganic" as well as of the "organic" energies of organism, so that *à priori* a phyletic classification might be based upon the physical or the chemical phenomena. But how much has been determined of the evolution of physical and chemical energies ? Certain of their present actions are becoming explained, by gradual synthesis many compound substances have become built up, and in change in the substances possibly the physical movements of these substances become changed; but are there facts to show that all substances have been derived from one primeval substance, or that all kinds of physical motion are referable to one ancestral kind ? The uncertainty on these points, the lack of relatively positive facts, the great hiatus in our knowledge of physical and chemical relations as studied particularly in organisms, are sufficient reasons for neglecting at the present time any attempt to base a phyletic classification of organisms upon such relations. Until all the phenomena of growth and structure in organisms can be expressed in purely physical and chemical terms, which so far has not been possible, it would be incorrect to build upon classifications which would neglect many of the energies and phenomena of organisms which particularly distinguish them from non-organisms.

There then remain to be compared the morphological, physiological, ecological and psychical classifications, and to be determined which of them can be most profitably employed in tracing the course of evolution. All these are closely related, for the nervous system, *e. g.*, shows a structure, a function, a relation to habits and environment, and to so-called mental phenomena. The living structure and its activity are inseparable, and both have close connection with the environment. The fact that they are all so closely and inseparably correlated that in treating of an organism the naturalist is obliged to regard it in all of these aspects, would argue that a classification might be based equally well upon any one of them. Much more has been determined in regard to structural than to physiological, psychical or ecological relations of organisms, so that a morphological classification, having more facts at its command, is at present more practicable than any other. In time the morphological classification must be tested by the others, and now no phyletic classification is justifiable which would not regard the functions and the interactions to the environment, for these have modified the structure. Function has produced structure, and structure so formed in turn tends to restrain change of function, and the stimuli of the environment are the strong masters of the organism. Hence structure, function, relation to environment, each mirrors the others, any one of them might be the basis of the classification; and if we now select the morphological characteristics as the basis for determining the phylogeny, it is because they offer us at present the richest material. But starting as we do with a classification based upon similarities determined on structure, we are not to consider that on structure alone our ultimate phyletic classification is to rest; for to understand the phylogeny of organisms we should not view them as seen in certain instants of time only, but must explain the continuous change that has occurred between those instants by analyzing the phenomena of growth and of reaction to environmental stimuli. The phenomena of structure, when the comparisons have been rightly instituted, may go far toward explaining the path of evolution, but the change produced by evolution, which is equally necessary for our ideas of phylogeny, can be determined only by considering in addition the energies and activities of organisms, and their interaction with the environment.

II. The Individual.

Organisms are living entities, yet, since each organism is known to be composed of parts, there arises the necessity of determining the degree or kind of individuals that are to be classified. In Nature occur only individuals, as was clearly pointed out by Lamarck, and is generally acknowledged at the present time, species and other groups being arbitrary concepts. Hence it is individuals that are to be classified and mentally arranged into groups characterized by similarity of structure; but before this can be done it is necessary to decide what is meant by the term " individual."

The primary idea of an individual is independence, as in saying " an individual is that which is capable by itself of performing all the activities necessary for its existence" ; or " that which cannot be subdivided without ceasing to be." But neither of these statements are quite correct, for no organism is wholly independent of other organisms and of its environment, and experiment has shown (in cases of regeneration) that what are commonly known as individuals may be subdivided, and yet not cease to exist; the independence then is one of relative degree. Another criterion is that of structural disassociation: an individual is an organism structurally complete in itself, not a part of a larger structural whole; though in practice this definition is often found of little value, as in organisms forming corms and stocks, yet perhaps it is as far-reaching as any that can be offered. Another criterion would be the ability of reproducing itself through an ontogenetic cycle similar to that by which it had been formed. Yet, with this definition difficulties at once arise. For while, *e. g.*, the ovum of a bird, once fertilized, can form an adult bird containing ova in its ovary, the last-named ova are unable to give rise to a second generation of adult birds until they are first fertilized. And the adult hen bird cannot produce a new generation until its ova are fertilized by spermatozoa from the male. The ovum of a bird, deposited outside the body of the mother, would generally be regarded as an individual, and so would the adult hen or cock; but the ovum cannot reproduce itself without being fertilized, nor can the hen or cock reproduce themselves without mutual union of their reproductive elements. In other words, this criterion makes no allowance for the general occurrence of organisms which complement each other in ensuring procreation. It is doubtful whether any organism can reproduce itself indefinitely without at least occasional interaction with another organism; in the Metazoa the dioecious condition would appear to be the primitive one; accordingly, the lowest organisms at some period in their reproductive cycle, the highest organisms at each period of reproduction, need coöperation with complemental individuals in order to insure successful reproduction. Whether the complemental individuals are structurally alike, as in the Infusoria and hermaphroditic Mollusca, or whether they are structurally dissimilar, as in most dioecious forms, it would still hold that the single organism would not be capable by itself to reproduce itself. And again, accidentally infertile organisms or normally infertile organisms, such as the worker females of the Hymenoptera, could on this definition not be classed as individuals since they are unable to procreate themselves; yet, no one would maintain that an ox or a worker ant is not an individual.[2] Therefore this criterion of individuals, the ability by itself to reproduce itself, must be changed to "ability, on interaction with complemental individuals, to reproduce itself." But this definition will not enable us to determine the individuals to be considered in phyletic classification, as we shall proceed to show.

There are found among organisms, as has been so frequently reiterated, many degrees and kinds of individuals. For each more complex organism must be decided what is the higher individual, and what the individuals of lower grades. The ideas of corm, stock, person, organ, intergrade, sometimes for the same organism, almost always when we compare complex organisms of different kinds. Thus we may term "colony" or "corm" the connected individuals of the protozoan *Globigerina*, a proliferating Hydroid stalk, the unified bundles of spermatozoa of an Isopod Crustacean, or a compound Tunicate. And yet how these several organizations differ structurally! In the Tunicate organization itself a great series of "individuals" may be distinguished, as one will. Thus (1) a cellular individual, such as a chromosome or a centrosome; (2) a tissue individual, a cell; (3) an organ individual, a tissue or some specialized part of the organ; (4) what is generally spoken of as an organ, such as the heart or the intestine; (5) an organ system, such as the body wall; (6) what is generally regarded as the individual in this particular case, and (7) what is termed the corm. For the cytologist, the embryologist and the anatomist the idea of what constitutes the individual will differ. Likewise, there are many possibilities of interpretation of the organization of a Siphonophore; and in the case of a proliferating *Hydra* or *Microstomum,* it is practically impossible to decide at just what time two individuals appear in the place of the original one.

---

[2] This objection to the definition is not, however, perfectly fair, since in classification we deal with normal and not accidentally mutilated organisms, and since a worker ant may in one sense be considered embryonic, because its genital organs and ova do not attain a complete development, but are arrested in their growth.

All the preceding bears out what each naturalist finds in his own experience, that there occur many degrees of individuals, and that a sharp definition to cover all cases is practically impossible. Perhaps the nearest to it is found in the idea of structural disassociation, though this too breaks down when we consider the various kinds of corms and colonies found in organisms, and the cases of intimate symbiosis (such as the Turbellarian *Convoluta* with its enclosed plant cells). And yet to work upon our phyletic classification, it is necessary to know what are the individuals which should be the materials of the study; perhaps they may be more closely determined by the following line of reasoning.

Progressive evolution is a change from the more simple and generalized to the more complex and specialized in both the individual and the race. In the evolution of the race we consider the organism as a whole. This gives us the working criterion of individual, which is concisely the largest disassociated whole. And it is in this sense that the term individual is generally employed by phylogenists—that is, "individuals" are the units which make up our concept of "species," as the latter term is usually employed by naturalists. This definition will not apply to all cases, as, for instance, certain corms; but in many, if not all, such cases the "individual" and the "colony of individuals" may be eventually distinguished by comparison of undoubted single individuals with corms of united individuals of genetic affinity with the former. And it is necessary wherever possible to distinguish an individual from a corm, so that relatively similar units may be compared.

III. THE ORGANISM AND THE STAGE AT WHICH IT IS TO BE CLASSIFIED.

For purposes of phylogenetic classification it is perhaps best to regard "organism" as synonymous with "individual"—*i. e.*, the largest disassociated whole. Yet under the idea of "organism" have been grouped living units of different values, just as we have seen to be the case with the idea of "individual." And on this account it is necessary to see what these degrees of organisms are, and why a particular degree of organism should be made synonymous with a particular degree of individual.

In a multicellular animal parts of a cell have been regarded as organisms. Thus Altmann has considered certain granules, which according to him compose the living substance, to be each of them separate organisms, so that the cell would represent a symbiotic state of many organisms.[3] The centrosome is frequently spoken of as an organism, and by Eisen the nucleus, the cytoplasm and the attraction sphere have been regarded as three distinct organisms in a state of symbiosis. Chromosomes, by those who have corroborated the original position of Boveri, are looked upon as cellular individuals, though it is recognized that these elements stand in intimate functional connection with the rest of the cell. But what concerns us here most particularly is the standpoint of those who consider the multicellular animal to be an aggregate of organisms, the cells; and the view which regards an Annelid to be composed of a chain of organisms, its metameres or segments, or a Cestode to be made up of a row of organisms, its proglottids.

Now these various degrees or kinds of "organisms" would not be so confused if a distinction were drawn sharply between "organism" and "element of an organism." Under "organism" we should then understand "the largest disassociated whole," and its parts, as organs, tissues, cells or parts of cells, would be the "elements" which compose it. Whitman in his paper, *The Inadequacy of the Cell-Theory of Development*, has pointed this out most incisively. There he shows that structure is dependent upon the general organization, not upon the particular nature of the cell components; acellular and cellular organs may be compared, unicellular with multicellular, and intracellular with intercellular. In other words, we might say that it is not the cells which make the organism, but the organism which makes the cells. This thought may be carried further: the cell contains particular parts or elements, such as chromosomes, centrosomes and cytoplasm, but is more than a mere aggregate of these; and the Annelidan organization contains parts, such as the metameres, but the latter are not separate organisms. Thus the Metazoan is not a mere symbiotic aggregate of cells regarded as individual organisms, but these cells are merely subservient parts of the whole organization. Under " organism " then we must consider the whole organization, if we would not confuse entities of different values; and for the parts of such organisms the terms " structural element " or " micro-organism."

---

[3] That the protoplasm of the cell is an aggregate of minute but visible separate granules, as Altmann endeavored to prove, has not been corroborated by the more careful studies on the cell.

The organization as a whole is, then, of primary importance, not its elements. And by employing " organism " to mean the " organization as a whole," we are justified in classing " organism " as synonymous with " individual," as defined above, namely, " the largest disassociated whole." It is the organism defined in this sense that is the unit to be treated in phylogenetic classification. It is necessary to be clear upon this point, and not to regard parts of cells, or cells, or tissues, or organs as the primary materials to be treated in classification. The organisms or individuals of our classification are then primarily the kind which are mentally grouped under what we generally understand as " species." And since a species is simply a mental association of similar individuals or organisms, it cannot be perceived; so that species are not the materials for classification, but the perceptible individuals or organisms which compose them.

This conclusion as to what are the organic units primarily to be classified is further emphasized when we come to consider at what stage of its life-history the organism should be classified. The organism may be treated at any or all stages of its cycle, in order to understand its structure and growth phenomena; but it must be determined at what stage it is to be classified, in order to show its phyletic progress.

Now classification must represent not only similarities of descent, but divergence from the original ancestor; must show how far each organism has progressed in its evolution. The stage at which it is to be classified, arranged in the genealogical system, would then be that of its perfected condition, for then is to be found its furthest degree of specialization. And to classify it at an earlier stage would be to neglect the full degree of its evolution. This is a conclusion of importance when we consider certain attempts to classify organisms considered wholly at embryonic and larval stages, as in the so-called "embryological classifications." No objection is made to consider organisms at any stage, as an ovum, an embryo, a larva, or an adult, nor yet to consider a particular organ by itself in any of these stages, for such examination is necessary for understanding structure and growth; but these considerations are preliminary to the phyletic classing of the organism, which must be done when it has attained its full development and is most different from other organisms. Organisms at their perfected stages are then the materials to be classified.

But it is difficult to determine just what is the perfected or mature stage of an organism. In general the period of reproduction may be said to be the perfected stage. This would especially be the case for many free-living organisms which die after reproduction, as the males of most insects immediately after copulation, and the females of many after oviposition. In these particular cases the organisms attain their fullest development at the period of reproduction, and die without passing through further structural phases. But in other free-living animals there are several periods of generation before the animal dies; and in some animals, as in certain birds, the dimensions of the body and the character of the plumage change with each reproductive period—that is, the size and color changes more or less with each prenuptial moult. And in mammals, those whose reproductive period may extend over several years, a gradual change of the whole organism takes place during this time, so that in the stage of its last reproductive period it may be quite different in its characters from what it was at the first. Also, in species with individuals capable of reproduction occur sometimes individuals with arrested genital organs, such as the worker Hymenoptera; for the latter reproductive activity cannot be considered the criterion of structural perfection or maturity. Then, in cases of neotenia, the reproductive elements may attain their full growth before the other parts of the body: the organism here is reproductively mature before it is somatically. Again, at the stage of reproductive activity the organism may be less differentiated structurally than at preceding stages, as in some extreme cases of endoparasitism. Where alternation of generations (metagenesis) occurs, there may be, as in the case of certain Hydrozoa, two generations, each reproductively active, and the individuals of which are structurally different: which of these is the perfected stage ? And finally, when it is recalled that for certain organisms there is a succession of stages of senility, it will be seen how difficult it is to define what is meant by maturity or perfection of organization.

We have just seen that the period of reproductive activity does not always fix sharply the stage of greatest perfection of the organism. This stage, from the phyletic standpoint, is that when the organism has attained the end of the period which precedes senile modification. This may be the stage of greatest structural differentiation of the organism, or it may not. In the case of an extreme parasite, such as certain of the highly degenerated Cirripedes and Copepods, the larval stage may be the most perfect, from the standpoint of general structure, for then the locomotory appendages, sense organs and separateness of the metameres are clearly pronounced, while they degenerate later. But, if such a degenerate parasite were classified at its earlier, non-parasitic, more structurally perfect stage, such a classification would not represent the degree in which its evolution has diverged from that of its relatives, and would therefore rank the organism in a more primitive stage than it deserves. It is the end stage which shows how far the individual has proceeded in its evolution, whether progressive or regressive, while classification at an earlier stage, even though then the organism be structurally more complex, would not show the whole path of descent. Maturity, from the phyletic standpoint, is the stage preceding senility. It is not my purpose here to define senility, or what characterizes it, and indeed, senility may appear in one part before another has reached its full development, and at its first appearance is difficult to detect. But we would say that the organism as a whole is not senile so long as it continues the power of reproduction; and if there are several periods of reproduction, we should not consider the organism to be senile as a whole until after the last period. Thus, in the cases of birds which show successive nuptial plumages and structures, or of mammals which change more or less with each successive period of reproduction (as the male deer which multiply the number of prongs upon their antlers), it would be the last period of reproduction at which the individual should be classified. In a case of excessive parasitism, many organs of the body may have been in degeneration before the time of reproductive activity, yet the organism should not be classified before it is functionally reproductive. And it is correct to consider the organization as a whole as non-senile up to the time of the reproductive activity, since non-senile powers of growth are transmitted to its ova. In cases of complete successive hermaphroditism, where the individual is first functionally male, then hermaphrodite, then female (protandry), or where the succession is the reverse (proterogyny), the terminal stage also would be the one at which the individual should be classified, even though, as in many pulmonate Gasteropods, certain organs have during the reproductive period become degenerate (as the genital organs characteristic of the first functional stage).

Accordingly, in cases where alternation of generations does not occur, the mature or perfected stage from the phyletic standpoint would be found not before the last reproductive period. Generally it would be at that last period, if not always. For even in the case of neotenia, where the reproductive cells are mature before the somatic structure is fully differentiated, such procreative precocity in parasites is evidently only an adaptation to accidents inducing a precocious departure from the body of the last host (as in *Gordius*), and as a rule the soma has time to differentiate fully before the reproductive elements are deposited. In mammals, neotenia may be said to occur, since considerable somatic differentiation takes place after the first period of reproduction; but in mammals the case of neotenia need not perplex us, since, as has been shown, a mammal is to be classified at the time of its last reproductive period. The organization as a whole is then non-senile until after the last reproductive period; the individual is to be classified at that period, and not before, for classification at a preceding state would not show the full extent of its development. Classification after that stage is not permissible, unless for some cases of neotenia, since cessation of reproductive activity denotes the beginning of senility (catalysis of the organization as a whole), and since after such cessation further changes of the organism could not be transmitted to the offspring.

There remain to be considered the cases of alternation of generations (metagenesis), where the individuals of one generation differ structurally from those of the next generation, as in many Hydrozoa, where from the polyp is produced a medusa, from the medusa a polyp. Each generation here is reproductively active, so that the state of such activity does not decide for us whether the classification should consider primarilythe polyp or the medusa condition. Now, in the Hydrozoa many variations are found in the cycle of generation. *Hydra* can produce new polyps asexually, by budding, and also by fertilized eggs, *i. e.*, sexually; here there is change of generation, but not polymorphism of the successive generations. In certain Hydromedusæ there is true change of generation, with free-swimming medusæ budded off from the polyp individual (" metagenetic " Hydrozoa); in others the change of generation is not so clearly marked, but the medusoid individuals remain attached to the polyp as medusoid buds or gonophores (Hydrozoa with masked change of generation); in still others there is no polyp stage, but a medusa develops from the egg, and the latter becomes another medusa (" hypogenetic " forms, with suppression of one generation). Again, while most medusæ are incapable of asexual division, and reproduce by ova and spermatozoa, certain of them reproduce also asexually, by budding. In the Hydrozoa is found a fund of differences in the degree and kind of generation, such as no other metazoan group evinces (not even the Trematoda), and on this account they furnish a broad field for examination. Now in such Hydrozoa as show no change of generation, the individual should be classified at its last stage of reproductive activity, in order to represent its degree of racial development. Where true change of generation occurs and the different generations are separated individuals, such individuals should be classified as stand at the end of each metagenetic cycle. This is a consequence of the argument given before, to show that the organization as a whole is most advanced and perfect, and therefore expresses most fully the phyletic divergence of the organism from its ancestors, at the time of the last period of reproduction. Where the change of generation appears less pronounced, by reason of the egg-producing individuals remaining attached as gonophores to the body of the polyp, the same conclusion would hold—*i. e.*, that the egg-producing individual should be the one classified, provided that such a medusoid bud or gonophore be sufficiently specialized in structure from the polyp condition to be regarded as another individual and not merely a part or organ of the polyp. For, granting the correctness of the general view that such gonophores represent modified medusæ, which at an earlier racial period led an independent, free-swimming existence, they may in extreme cases lose all the original medusoid characters except that of producing eggs, show no independence of the polyp stalk, and, in fact, be more correctly considered organs (gonads) of the latter than separate individuals. This would be a case where a part once cut off as a separate individual with an independent existence has been gradually reduced to the state of an organ. In such a case, then, where the gonophore shows no independent existence, but is a part of the polyp stalk, the whole organization—*i. e.*, the polyp stalk with its gonophores—should be the one classified, because all together represent one organization. This whole organization should be classified when its reproductive organs, the gonophores, are in functional activity, that being the period of the greatest perfection of the organism. The difficulty in putting this principle to practice is to be found in those cases where it is hard to determine whether the egg-producer is to be considered an independent medusa or an organ of the polyp stalk. But at present we are considering only the principles of classification; two processes or states which in their extreme conditions are easily separated, are often found in natural phenomena to be connected by gradual steps; this is to be expected in any gradual evolution. Each case difficult of decision must then be considered in turn.

The principle, then, in cases of pronounced change of generation, where the successive individuals are structurally different, is to classify the organism at the end stage of each cycle. A cycle is in a sense a circle, without beginning or end; yet a little thought convinces that there must have been a commencement to every cycle. In the case of a Metazoan, where from the egg develops the mature organism, and from that an egg again, we commonly speak of the mature organism as the end and the egg as the beginning; and with right, since development is from the more generalized to the more specialized. Or regarding only the germ-cells of a Metazoan, apart from the soma, we find also a cycle: *n* generations of ovogonia, a stage of synapsis of the chromosomes, a stage of maturation, a stage of conjugation (fertilization), all constituting one cycle, which is followed by another like it. This germinal cycle too must have had a commencement, and, as I have attempted to show elsewhere, the period of fertilization (conjugation of ovum and spermatozoon) is to be considered the starting point. In the case of change of generation for the particular objects under examination, the Hydrozoa, the polyp stage is generally regarded as the beginning, and the medusa as the end of the cycle. This has its justification, for the medusa is more complex in structure than the polyp, that is, has passed through a longer ontogenetic stage. Here, too, however, the cycle really begins with the fertilized ovum, and ends with the stage that produces ova, if we would draw a parallel to the germinal cycle of Metazoa. In the metagenetic Hydrozoa it is the medusa which produces the ova. If, on the other hand, greatest complexity of structure should not coincide with the end of the reproductive cycle, such complexity would of course not be a criterion of this stage of the cycle, which nevertheless should be the one classified. Such a case would be an organism with change of generation, but with a regressive development in the latter part of its ontogeny (as might be induced by parasitism), so that the terminal stage would be less complex than some preceding one. No such case is known, however; so that with the facts at hand we are justified in concluding that greatest complexity of structure is the test of the last stage of the cycle in alternating generations; and it is that last stage which is the one to be classified.

IV. The Classification of Polymorphic Individuals.

In the preceding section have been considered such polymorphic individuals as succeed each other in alternation of generations. In many species are found together in the same generation individuals which differ from each other, as either in sexual dimorphism or in polymorphism. The former shows the distinction singly of males and females, and is found in dioecious species; while the latter shows the males and females in several different forms (as the polymorphic Hymenoptera). Polymorphism also may show in the same species a distinction of sexual from asexual individuals, as in certain corms. Sexual dimorphism and polymorphism are the results of a division of labor between the individuals of a species, as the structural differences in the parts of one organization are due to a similar specialization between them; in the one case the units are individuals, having physical disconnection, while in the other they are not individuals, but parts of one whole. In the former they compose not a perceptible but a thinkable whole, which we term a species.

The question is, accordingly, where the individuals of a species are heteromorphic, on which of them should the classification be based ? On the males or on the females, on the sexual or the asexual individuals ? Our classification must start with the single individual, and proceed next to an arrangement of the individuals into those lowest groups known as species. If all the individuals of a given generation of a species are monomorphic, the consideration need not pass beyond any one individual, for each individual would show the full characteristics of the species. And since this is not the case in species in which the individuals are heteromorphic, in such species all the component individuals must be studied before the species can be mentally defined. In other words, while individuals are the primary materials of classification, species are the primary group units and so must be defined as to include all the kinds of individuals composing them.

Starting then with the principle that individuals are to be first considered, and that a classification of the most primary groups—*i. e.*, species—demands a knowledge of all the individuals which compose such species, we must not in classification neglect the consideration of any individual. Therefore classification must be based upon all individuals, since otherwise our concepts of the lowest group would be incomplete.

To the systematist are known many instances of species with sexual dimorphism, where the individuals of one sex are less variable than those of the other with regard to closely related species. Thus among the insects, the females of Disptera are, as a rule, difficult to distinguish specifically, while in the less conservative males specific characters are much more clearly pronounced, and in this particular case much of the classification has been based upon the genital armature of the male.[4] In birds also the males generally show greater differences than the females; this is observed also in many mammals, as the Cervidæ, in the Gordiacea, and in numerous other groups. But while a description of a new species is in practice often based upon individuals of one sex, in cases where those of the other sex have not been seen, yet such a description is only a partial characterization of the species, for the complemental individuals have been neglected; it is not, strictly speaking, a description of a species, but of only one kind of individuals of that species. Now, let us consider two species, A and B, each with sexual dimorphism, the females of the two not appreciably different, while the males show marked differences. Then on comparison of the females alone, one would conclude that they composed only one species; of the males alone, that they composed two perfectly distinct species. The error of basing the characterization upon either sex by itself is then obvious, for A and B are neither one species, nor are they *clearly* distinguishable species; the similarities of the females of the two show that the species are very closely related, while the differences of the males show that they are nevertheless distinct. The species would then be characterized, "females indistinguishable, males differing in such and such characters."[5]

---

[4] If the genital armature of the female, which is to greater or less extent adapted to that of the male, be examined more thoroughly than it has at present, perhaps it, too, would afford good specific distinctions.

This reasoning, based upon cases where neither sex is markedly degenerate, may be, to a certain extent, a guide also for such cases where either the male or the female is degenerate in comparison with the other sex. Such cases are numerous, as the degenerate character of the male in the Rotatoria, in the Echiurid *Bonellia*, the marked sexual dimorphism in the Coccidæ and some parasitic Copepoda, etc. If in these the classification were based upon the more degenerate individuals, the species would be ascribed too low a phyletic rank, and if upon the less degenerate alone, too high a rank. For here, as for the other cases, the characterization of a species must be the sum total of the characterization of its different individuals. In such a species the male and the female may have had a corresponding ontogenetic development up to a certain point, then the one developed regressively and the other progressively, a difference in mode of life being the determining factor

---

[5] In the particular case used for discussion we have excluded the possibility of the occurrence of two kinds of males complemental to a single kind of female, *i. e.*, dimorphism of the males. When females appear indistinguishable, however, after a thorough study of all their parts, while the males are easily distinguished, the classifier should disprove that it is not a case of male dimorphism before he founds two species.

(as it probably is in most cases of sexual dimorphism in the lower animals). If both sexes had a parallel ontogenetic development, we should not hesitate to classify the individuals at the terminal stage of their reproductive activity, whether the development had been progressive throughout or in part regressive. When there has been a divergence in the ontogeny of the two sexes, the males and females being complemental individuals, the species contains both progressive and regressive individuals, it is to be classified at the time of reproductive activity of the two sexes, and is to be ascribed a rank intermediate between that of the conditions of the two sexes.

Unless this principle of considering all the kinds of individuals in a species be strictly enforced, great confusion would ensue in the ranking of a species, depending as to whether the classifier considered the males alone or the females alone, or asexual individuals alone, or all together. It is necessary that all the individuals of a species be known before such a species can be thoroughly characterized, and for only a comparatively few species of certain animal groups have such broad definitions been given.

It will of course be understood that the writer does not imply that species would be perceptibly delimitable, were it not for the extinction of or our lack of knowledge concerning intermediate species. "Species" is a mental concept for a primary group of individuals of the closest genetic connection. If in any phyletic series we could know to-day all intermediate stages, so that the whole would be a continuous line of development, and assuming that such a development were perfectly gradual, nevertheless we should have to project the concepts of species into that whole, arbitrary though such concepts would be, in order to secure certain fixed points for observation and interpretation. Thus we study a section through the body of an animal if we cannot understand this animal in its entirety, and by supplementing our knowledge with sections from other regions of the body gradually reconstruct the whole. A species is a mental section of a line of evolution, and is necessary to enable us to interpret the whole. That is what is here understood by the determination of a species. Where, through extinction, we find disconnected species, we have sections made for us by Nature.

V. THE KINDS OF HOMOLOGIES.

Before considering the methods of treatment of structural characters, and comparing the anatomical and embryological methods of determining genetic relationships, it will be well to discuss briefly the kinds of structural relations known as "homologies."

The working principle of the phylogenist who is studying a line of development represented to-day only by fragments, and who has not the resource of fossil remains of the extinct members of that line, is that similarity in essential particulars denotes genetic affinity. This principle would seem the more probable the more complex the organisms treated, for it would not be probable that two complex forms from very different beginnings could come to resemble each other in all particulars. The less complex and more plastic the organization, the more complete could be the convergence of structure. This principle is a necessary postulate, and though it remains to be thoroughly proved, yet it is allowable so long as the known facts do not contradict it. Without its aid no phylogenetic conclusions would be possible.

There have been distinguished various kinds and degrees of structural similarities or homologies. Owen, in his *Lectures on Vertebrata,* 1846, defines: "*Analogue,* a part or organ in one animal which has the same function as another part or organ in a different animal. *Homologue,* the same organ in different animals under every variety of form and function." This distinction, generally accepted to-day, terms "analogical" a similarity of function, and "homological" a similarity of structure. He distinguishes further three kinds of homological relations. *Special homology,* "correspondency of a part or organ, determined by its relative position and connections, with a part or organ in a different animal; the determination of which homology indicates that such animals are constructed on a common type." *General homology,* "a higher relation of homology . . . . in which a part or series of parts stands to the fundamental or general type. . . . . Thus when the basilar process of the human occipital bone is determined to be the 'centrum' or 'body' of the last cranial vertebra." *Serial homology* or *homotypy,* the relation of segmentally arranged parts of the same organism. "In the instance of serial homology . . . . the femur, though repeating in its segment the humerus in the more advanced segment, is not its namesake—not properly, therefore, its 'homologue.' I propose, therefore, to call the bones so related serially in the same skeleton 'homotypes' and to restrict the term 'homologue' to the corresponding bones in different species.[6] And in his paper *On the Archetype and Homologies of the Vertebrate Skeleton*, in 1848, he states: "Homological relationships . . . . are mainly, if not wholly, determined by the relative position and connection of the parts, and may exist independently of form, proportion, substance, function and similarity of development."

Owen implied by "homology" an essential agreement in structure and connections, a relation of essential structural agreement. But, as Cuvier before and L. Agassiz after him, he held the view of the occurrence of different plans or types of structure among animals which could not intergrade and were not gradually evolved. Under the present dominance of the theory of descent, the idea of separately created "types" or "plans" has been relinquished, so that while we retain the term "homology," we define it as a relation of genetic descent.

Of the kinds of homologies distinguished by Owen, the *general* and *serial homologies* are of not the same direct value to the phylogenist as the *special.* Relations of two sides of the same body to each other, of anterior to posterior end, of one antimere or metamere to another, of the right arm to the left arm, or of an arm to a leg, etc., are all relations between the parts of one organism. In phylogeny we are immediately concerned with the relations of different organisms, and with general homologies, including under that term also serial homologies, only in so far as they serve to explain the former. With the treatment of structural characters we shall have to consider general homologies, and now simply mention some kinds of special homologies.

Under the idea of "special homology" is now generally understood a relation of genetic affinity. "Homologie nennen wir eine Uebereinstimmung, die auf gemeinsamer Abstammung der betreffenden Organismen beruht. Der Ausdruck Homologie wird demnach vollkommen im Sinne der Homophylie gebraucht."[7] And so we must employ it, with the working theory of "unity of development" in the place of the earlier "unity of plan." In order to understand the relations of two organisms as wholes, it is generally first necessary to commence by comparing them part by part; the correspondence of one part in organism A with a similar part in organism B is a special homology, when interpreted as a proof of genetic affinity. A special homology is then our interpretation of the similarity of the parts of two organisms as denoting homophyly, or likeness of genesis.

---

[6] Vicq d'Azyr was the first recognizer of serial homology: *Parallèle des os qui composent les extrémités,* Mém. Acad. Sci., 1774.

[7] Hatschek, *Lehrbuch,* 1888.

Various degrees of special homologies have been distinguished. Thus Gegenbaur:[8] *complete homology,* when the organ in position and connection is retained unaltered; *defective,* when a part originally present has been lost; *augmentative,* when a part not originally present is added; *imitatory,* as when one metamere produces a structure characteristic of a metamere further anterior or posterior (the three last being classed by Gegenbaur as *incomplete* homologies). Frequently also the distinction is made between *adult* and *embryonic* (or *larval*) homologies, a distinction based upon the stage of the individual in which the homology is determined. Another grouping of homologies, due mainly to the study of cell lineage, is *actual homology,* when at the stage considered the relation is found; *prospective,* as when two blastomeres (of different organisms) are considered homologous because they give rise to similar organs in the adults; and *retrospective,* as when two adult parts (of different organisms) are considered homologous because they are derived from corresponding cells or regions of the embryos (or larvæ) of these organisms. Still further classifications of homologies are possible, but these are sufficient for our present purpose.

Under the idea of "homology" we shall then understand "homophyly," and restrict in what is to follow the term "homology" to the idea of "special homology," unless otherwise specified. In the determination of homologies we may proceed with the adult structure (the anatomical method), or with the embryonic or larval structure (the embryological method). And we shall have to decide, if possible and without bias, which of these methods is the correct one: the one of Owen which lays stress upon the adult relations of structure, or the one which lays primary importance upon ontogenetic similarities, and has been defined by Darwin[9] as follows: "*Homology.*—That relation between parts which results from their development from corresponding embryonic parts, either in different animals . . . . or in the same individual."

---

[8] *Vergleichende Anatomie der Wirbelthiere,* I, 1898.

[9] *Origin of Species,* Glossary

VI. STRUCTURAL CHARACTERS, AND THE DETERMINATION OF THEIR RELATIVE VALUES FOR PHYLOGENETIC CLASSIFICATION.

The confliction of the judgments of different morphologists in regard to lines of evolution is due to the differences in their opinions as to what structural characters should be used as the basis of comparison. If there were some well-founded principle in determining the relative values for phylogeny of such characters, the number of points of view would be lessened and greater agreement thereby attained. But, as the case stands to-day, with each new point of view ideas of phylogenetic relationships are changed; and since in those whose standpoints have become fixed there is no adoption of the new points of view, the latter simply bring in additional schemes of classification, and will continue to do so until all possible points of view are exhausted. This oncoming of new interpretations is of the highest value in the study of morphology, and he sees best who can, unbiassed, consider facts under many standpoints. A new interpretation is a light strong in proportion as it is maintained by the facts. Yet too often the conclusion is reached before the thinker has taken time to consider the objections—before he has sought to prove his conclusion by first trying to disprove it. There is in every worker more or less of a tendency to defend his point of view and to be slow in relinquishing it; and this is good for the clear expression of the point of view, but bad for the thinker and his science when he continues to abide by it after it has been disproved. Each new point of view is to be welcomed, since we cannot say which one is right until all have been examined, provided that it has not been hastily conceived.

In the following we shall endeavor to express certain principles in the search for homologies, and to determine the general method in the search for them; bearing in mind that it is simply an attempt to reduce the confliction of opinion, rather than an essay of a new point of view.

(*a*) *The Organization and its Components.*

In Section III it has been shown that the organism is not a colony of relatively independent units, but is one whole containing parts; and that the whole gives its impress to the parts, rather than the parts to the whole. And then it was shown that an " organism " and an " organization," both terms being employed in the broad sense, are synonymous.

The organization being then one closely united whole, we reach the principle that the organization as a whole must be studied; and hence that any scheme of classification based upon one kind of organs alone is erroneous in its method.[10] The truth of this is further borne out by the following reasoning: The organization being one closely connected whole, there is a perfect physiological and morphological correlation of its parts; and although some of them have a greater value to the whole economy than others, yet each part is dependent upon the others. The parts are not individuals, in the sense in which the individual has been defined (Section II), since they are normally incapable of separate existence.[11] When we say " a gland cell of the intestine of a snail," we speak in succession of a part of a larger part of a whole. Not only from physiological facts does this correlation become apparent but from morphological as well, for none of the parts show sharp demarkations. A vertebra of an adult mammal might be considered at first as a well circumscribed part; yet besides being one of a series of vertebræ, all developed from one anlage, its fibrous sheath passes over gradually into the tendons of the muscles attached to it, and its nerves and blood vessels are mere portions of the nervous and vascular systems of the whole organization. Similarly with a limb, a sense-organ, a lung, etc. For none of the parts of the whole organization can sharp boundaries be found; even the cells are either connected by a fusion of their contiguous membranes or processes, or by a common intercellular substance.[12]

The parts of the organization are then not individuals, since between all the parts exists the closest correlation; and the " largest disconnected whole " is the organism of phylogeny. Further, no part can be understood alone by itself, but the place which it occupies in the whole organization must be considered.

It is not to be wondered at that the parts of organisms are not easily delimited, since they are but local specializations of a whole. And the relative kinds of parts intergrade, so that it is purely arbitrary to distinguish, *e. g.*, between organ and organ system, between metamere and region, etc. Though it is necessary to give distinctiue names to particular parts, for purposes of description, it must be kept in mind that the parts or " organs " in being not sharply delimitable are purely arbitrary distinctions. Thus, an " organ " is more of a concept than an organism, since it is not so perceptibly delimitable; though less of a concept than a species, since the connection of its components is perceptible.

---

[10] A case in point is Huxley's brilliant paper *On the Classification of Birds*, 1867, wherein birds are primarily grouped according to the structural characters of one region of the skull.

[11] The germ cells, however, in their mature stages come under a different point of view, for they are then individuals of a second generation which have not yet left the body of the first. In the present discussion, when not otherwise stated, only the somatic parts are considered.

[12] The migratory cells of the body of Metazoa show perhaps more independence than the other cells, yet they too are influenced by the state of the organism as a whole; and even such blood and lymph cells are normally incapable of existence outside of the organism.

In one organization we find the general body plan, the major parts which compose this, and the minor parts which compose the latter. In a radiate body plan, as shown by a star-fish, the body is composed on the principle of converging rays, the antimeres; each of the latter is bilaterally symmetrical, with a distinction between dorsal and ventral, and contains a series of " organs "; and each of these organs has its minor parts. In a trematode there is a bilaterally symmetrical body plan, without antimeres; in an annelid, a bilaterally symmetrical united with a metameric, the larger parts being here the segments or metameres. Other body plans are the monaxonic, where there is more or less strictly radial grouping of the parts along one long axis; and the homaxonic, very rarely found, where all the axes passing through the central point are of equal length. But still other distinctions of body plans are possible. Thus: that in which the two ends of the body are dissimilarly developed, as head and tail, which might be known as the antipolar; where the body axis is straight and where it is bent, (Homaxonic and Heteraxonic, Hatschek); and various others which may be arbitrarily distinguished. Therefore there are many kinds of general body plans.[13] Of the major components of these body plans we may distinguish antimere and metamere, anterior and posterior, right and left, dorsal and ventral, etc. The major components of the latter are what are generally called " organs," such as nephridia, nerve cords, gonads, gills, etc.[14] There are finally parts of these organs.

---

[13] Though we use here the term body plan, we cannot any longer restrict its use to that of Cuvier, von Baer, and L. Agassiz; the four fundamental body plans distinguished by these naturalists represented to them four separate *fiats* of creation, which were unbridgeable. In the light of modern Phylogeny we know that animals were not created separately in four separate moults, and know that gradations are found between the different body "plans" or "types."

Now we find from this brief examination that there are different degrees of structural parts in the organization, beginning with the general body plan and proceeding to the minor parts which compose it. Shall the relationship of two organisms be determined by the comparison of their body plans, or of their major organ complexes, or of the smallest complexes ? And how is this comparison to be carried out, and on what kind of parts is the comparison to be instituted ? We may immediately proceed to the discussion of these questions.

(*b*) *The Criterion of Morphological Value.*

It is not justifiable to give any *à priori* decision as to what parts are of value in determining questions of relationship, since the criterion must be empirically sought.

As essential similarity is interpreted as denoting genetic affinity, so also there is a second principle in determining phylogeny, namely, that conservatism or fixity of a structure implies morphological value. By conservatism or fixity is implied the continuance of a part with relatively little change through a long line of evolution. If in a line of evolution leading from a type of organization *A* to a type *N*, a certain structure should be found in *N* little changed from its appearance in *A*, it would be called conservative; if it had become much modified or even lost before the stage of type *N*, it would not be conservative. The value of a structural characteristic for phylogenetic purposes depends directly upon how fully it conserves ancestral characteristics, and the less completely it conserves them the less value it has. This is the well-based working procedure of the phylogenist. A character which leads far back into the ancestry is the guiding line in interpretation of descent. If, through the continuous change which a race of organisms undergoes during the process of evolution, a particular part becomes much less rapidly changed than the others, that part certainly represents the ancestral characters most fully, and for the phylogenist its persistence or conservatism is the criterion of its morphological value. A character which persists through a very long racial period must do so by virtue of being of particular value for the economy of the organization, or for the perpetuation of the race. Structures of less value are more readily modified, or substituted, or even lost.

---

[14] "Organ" is employed in comparative anatomy in a very loose sense, as is necessitated by the practical impossibility of sharply distinguishing the intergrading kinds of structural elements. As generally used for the Metazoa, it is not applied to an antimere or to a metamere, but to more segregated portions of them. Physiologically, it is a part with a particular function to perform ; morphologically, a specialized part of particular structure. While no sharp definition is possible to cover all cases, we find that "organ" is generally employed by phylogenists in the sense of "the largest specialized part in an organization performing a particular function"; thus the respiratory organ of a vertebrate would be not a lung cell, but the whole complex of lung cells. And it is well to define the various degrees of structural parts as closely as possible, in order to compare in different animals only such parts as relatively correspond.

It is then clear that the first step to take in determining the characters on which classification should be based, is to find out the relative stability or conservatism of these characters, at the same time recalling that no characters should be neglected in the examination, but that they be ascribed value in the order of their conservatism.

The ever-recurring problem to the classifier is that of determining the interrelationships of, *e. g.*, these organisms, *A*, *B* and *C*, when *A* agrees with *B* in character *d*, but differs from *B* in character *e*, while agreeing with *C* in character *e* but differing from *C* in character *d:* is the value of character *d* of greater or less value here than that of character *e?* The answer may be a purely arbitrary one, such as would best suit the classifier's preconceived views; or it may be made less arbitrary and more logically precise by the application of the principle of conservatism as denoting value.

The application of this principle would seem at first sight very simple, but in practice it has been found very difficult. For in a racial progress, as Kleinenberg has shown so well for the individual development, one organ may become gradually substituted for another, so that it is difficult to decide at what point the first disappears and the second takes its place. A case in point is the substitution of one kidney system for an earlier one, and of a third for the second, in the evolution of the Vertebrates. In this case a persistence of the first kidney (pronephros) is found even when the second kidney (mesonephros) has been substituted in its place, and even in the organization showing the substituting third kidney (metanephros) a small portion of the first is still retained. The case becomes more difficult to interpret when not separately arising parts succeed each other, but when in the progress of the race from an early ancestral organ of diffuse arrangement one part changes into one set of organs, another part into another set. Thus from the gastrovascular system of a simpler Cnidarian with, *e. g.*, a structure like *Hydra*, are found in higher forms developing intestine and gonads (*e. g.*, Turbellaria). In all such cases where the substitution of parts is gradual, it is obviously difficult to determine where one organ ends and another begins, and hence to determine how far back into the phylogeny an organ extends. And the substitution is generally gradual, so that the new organ either arises from a part of the first, or the first becomes gradually moulded over to form the new; much more rarely is the first completely lost (ontogenetic development of the Diptera). It is not probable that a part in any case is completely lost without first aiding in the formation of another part; and this is the more true when we consider that accidental mutilations are probably not inherited. And further, it must be borne in mind that a character which is essentially conservative throughout one group may be variable in another: thus the external cuticle is comparatively uniform in structure throughout the Nematoda, but very variable in the Gordiacea (in some species of which it differs even in the two sexes).

A word may be said just here as to the value for classification of the statistical study of individual variation. The examination of the relative amount of variation in different parts of the same species shows of course which are most and least variable. It shows also that in some species there is less general variation than in others. The modern school of statistical variation has not brought to light any new points of view, but it has the advantage of deriving its statistics from a large number of individuals, and of reproducing these statistics in concise mathematical forms. Before its oncoming observers contented themselves with such loose expressions as "very variable" "slightly variable," etc. The accurate recording of individual variations is the scientific method of showing which parts are most conservative, and a character (*e. g.*, number of joints in an antenna) which has been shown to be very variable cannot be regarded as of much value; that is to say, such a character should be considered of little value in the diagnosis of the species. Yet in closely related species such a character may be eminently stable, so that in general no deductions can be drawn from these variation statistics to species other than those on which they were determined; they may be interpreted to show the mathematically probable further course of development of this species, but they do not show anything with regard to other species.

In one way this statistical study of variation may be of great service, namely, in regard to the distinguishing of " varieties " or " races " of a species. If the degree of variation between the individuals in one and the same portion of the area of distribution of a species be fully as great as the degree of variation between the individuals at the most separated points of this area of distribution, then it is not permissible to speak of " varieties " within such a species. Or, conversely, it is only allowable to distinguish " varieties," when in a portion *A* of the geographical area of a species the individuals show a different average of variation than in a portion *B*.

Davenport[15] has pointed out that the plotting of variation curves affords a criterion by which varieties may be distinguished from species, thus determining the indices of divergence—" if either of these indices is less than a certain number we have varieties; if above that number, species." But even with this method it is necessary to select a particular character as the " chief differential," and it is just with regard to this point that there is as yet no mathematical precision, and hence this method does not furnish a " precise criterion," though it is certainly a step in the right direction.

(c) *The Components of the Organization that are of Most Importance in Phylogeny.*

We have seen that the organization as a whole must be considered. The whole, however, can be understood only by synthetically considering the parts of which it is composed. These parts are of very different relative values, from the protoplasmic alveoli or microsome on the one hand, to the organ, organ system and general body plan, on the other. This leads us to the question, which category of parts should be considered in determining phyletic relationship ? Is it immaterial whether we base the classification upon cell structure, upon tissue structure, upon organ structure, or upon arrangement of the organs ? Or are there good reasons for using as the basis of examination a particular category of parts ?

---

[15] "A Precise Criterion of Species," *Science*, N. S. VII, No. 177, 1898.

To commence with the smallest perceptible parts of the organization, the components of the cell. A classification limited to these would represent the facts of cellular structure, and might be based upon the finer cytoplasmic structure, upon the number and nature of centrosomes or chromosomes, etc. But it is clear that such a classification, even if it could be consequently perfected, would be no classification of the organization as a whole, for it would neglect the structure and grouping of the more complex parts of the body. In thus affording no representation of the whole organization, it would be contrary to the conclusion that the organization (organism) as a whole must be considered, and hence would not be allowable.[16] The same argument holds also for a classification based upon kinds of tissues. These two possible modes of classification need not confuse the phylogenist, for they are logically incorrect.

There now arises the more difficult question. What particular category of the more complex parts of the organization should be considered ? Under these are the organs (as this term is generally used), the organ systems and the larger divisions of the body, such as antimeres, metameres, right and left side, etc. These being the larger structural complexes, their facts of structure show the organization as a whole, and hence on them the classification must be made. But should the facts of body plan, such as radiality or metamerism, be ascribed greater value than the facts of the organs which compose them ? Or otherwise expressed, is structure or arrangement of the parts to be first considered ? The answer to this must be empirically determined, and by determining which of the two is the more conservative, the structure of the organ or its spatial relations in the whole organization.

A little reflection upon the facts of comparative anatomy shows that " body plan " is generally very far from conservative. For, in the first place, different body plans or modes of arrangement of the parts are frequently found in different parts of the same organism. Thus in some Cestoda the scolex is more or less radial with regard to the arrangement of its parts, while each proglottid of the trunk may be bilaterally symmetrical (*Dipylidium*). In the

---

[16] Necessarily the Metazoa only are meant, for with the Protozoa there can be no other than a cellular classification ; yet, even in these, the organization as a whole must be considered.

Echinodermata there is a general radiate plan of the larger parts (antimeres), but each antimere may be bilaterally symmetrical, and the intestine, unlike the other organs, is not rayed. In the Anthozoa there is at once bilateral symmetry and radiality. In the Turbellaria are forms, which, in respect to the intestinal branches, are more or less clearly radial, and at the same time, with regard to the excretory and genital systems, more or less bilaterally symmetrical; and the Trematoda have a radial arrangement of certain organs, an unpaired (monaxonic) and bilaterally symmetrical arrangement of others. The metamerism of the Articulata does not extend to the intestine; and in the Gasteropoda a true bilateral symmetry may be found in the parts enclosed within the foot, while such symmetry is to great extent obliterated in the spirally wound superior portion of the body. There is, in fact, no animal known in which all the parts are perfectly bilaterally symmetrical, or all perfectly metameric, and only in certain Cnidaria does there seem to be perfect radial symmetry.[17] The facts being so, we are not justified in considering as of much value the plan of arrangement of the parts, or what is known as the "body plan." And another well-known illustration bears this out. Throughout the group of the Platodes (comprising the Turbellaria, Cestoda and Trematoda) there is a uniform type of excretory organs (protonephridia); but the external opening of these organs may be very differently situated in different organisms, and in closely related forms (of the Trematoda) these organs may be paired or unpaired.

There is a further series of facts to show that the relative positions of parts may be very different in closely related organisms; thus, the mouth opening and the genital apertures in the Turbellaria; the mouth opening sometimes on the right, sometimes on the left side in the Gasteropoda (even in different individuals of the same species); the position of the abdominal nerve ganglia in the Diptera, etc.

Such facts, which any comparative anatomist can multiply, show that the general plan of arrangement of the parts is usually far from conservative, and hence, judged by the criterion of degree of conservatism, is of little value for determining broader phyletic relationships. The body plan is easily influenced by the mode of life, as demonstrated by Lang and others; Lang has shown that radiality and sessility are often associated, a creeping motion and bilateral symmetry. Perhaps such a relation would be better expressed in the statement: the position of the mouth opening is determined by the mode of life, and the relative arrangements of the other parts become modified by change in its position. And there is another relation, also referable to the mode of life, namely, modifications of the arrangements of parts caused by the development of firm skeletal structures, as the shell in the Mollusca.

---

[17] Many of the Protozoa which were first regarded as of a perfect radial type, have more recently been shown to be asymmetrical in some respects.

In general, then, we may conclude that the modes of arrangement of the parts of the organization, which are known as radial and bilateral symmetry, the relation of dorsum to venter, etc., are characters of small degree of conservatism. But it is difficult to decide on the morphological value of metameric arrangement. For metamerism cannot be explained, as other modes of arrangement may be more or less satisfactorily, by the mode of life, but would rather appear to be referable to intrinsic growth methods; and it also does not become readily changed by variation in mode of life. Metamerism is also in no way a function of comparative size or length of the body, but would seem to be the consequence of primarily the mode of formation of the mesoderm (E. Meyer). Metamerism is more conservative than other body plans, and so must be given a greater value in classification. Thus the group of the Articulata is much better founded than the earlier postulated group of the Radiata, for it is based upon a more conservative mode of arrangement of the parts. And as generally held, metamerism of the inner parts is of much more morphological value than metamerism of the tegumentary structures, on account of the greater conservatism of the former.

The parts of the organization which furnish the best basis for classification are the organs, as this term is generally used. These parts may not reflect so fully the organization as a whole as do larger parts which they compose, such as antimere, metamere, right and left sides, head and trunk, etc.; but comparative anatomy has shown that they are, on the whole, more conservative, and on this account they are to be preferred. Their study, unlike study of cell or tissue components, gives a synthetic view of the whole organization.

The phylogenist has then to use what are generally called "organs" as the basis of his comparisons. And he has to determine by comparison which of the organs are the most conservative, and to grant them morphological value in direct proportion to their degree of conservatism. This must be done by a synthetic grouping of the facts, without any regard as to which organs are most convenient of study. He must also constantly bear in mind that an organ eminently conservative in one group may be variable in another. Degree of conservatism can be determined only by very broad and extended comparisons, and is to be gauged by the measure of change accompanying change of habit.

The great difficulty in putting this generally accepted principle in practice is the difficulty in determining whether the organs compared are homologous. Thus nephridia are organs of a certain function, but they are not of the same kind, not homologous, in all animal groups. Therefore they are not very conservative organs, even though they are present in many groups of animals. This is not, however, the place to discuss the organs in detail with regard to their relative morphological values: that would necessitate the reviewal of an enormous mass of facts. But it may be allowable to point out briefly those organs which seem of most importance in phylogeny. Omitting the intestinal organ, which is very readily modified by change of mode of life (as present in the female but absent in the male of Rotatoria), we find two organs of general occurrence in the Metazoa, the reproductive and the nervous systems. These are phyletically not as old as the body layers (ectoderm and entoderm), but both are found from the Cnidaria upward, and with fewer modifications than the body layers. Even extreme endoparasitism, the severest of all conditions, does not lead to the complete suppression of these organs. It cannot be stated that either of them is strictly homologous throughout in all Metazoa, for there is good evidence of substitution here, though to much less extent perhaps than in other organs. On the whole the nervous system, its central ganglionic portion, remains very conservative; and so does the central, gonadal portion of the reproductive system. These two are the most conservative of all organs, and their structure should receive first consideration in phyletic classification. The muscular system is as old as the nervous system, muscle and nerve are synchronous, but it is well known that the muscular system is very easily modified by change of habit. In the third rank would fall the organs known as nephridia or kidneys. The vascular, respiratory, locomotory, special sensory, intestinal, tegumentary and skeletal organs are all of less morphological value than these three for the determination of far-reaching relationships.

(*d*) *The Mode of Treatment of the Parts.*

The parts of the organization that should furnish the basis for morphological study leading to classification, we have seen, are those generally termed organs, and not larger complexes of these organs nor yet smaller parts of them. Broadly speaking, the organ is an anatomical unit in the consideration of the organism. And we have seen that it is necessary to fix upon certain parts for primary treatment, on account of the impossibility of mentally grasping the organization in its entirety. By examining in succession these components a synthetic concept of the whole organization may be gained. And all the parts must be studied—that is, the organization as a whole must be understood—before we can determine which of these parts are of most value for determining the phyletic affinities of that particular organization.

The mode of treatment of these organs is to compare those of different organisms, comparing together only those which evidently correspond anatomically. The more conservative organs would be the basis for defining larger groups, the successively less conservative for defining successively smaller groups ("small" being used in the sense of "closely related"). This is a well-recognized principle.

But great divergence of opinion is found in regard to the point of the mode of considering the organ, that is, which of its characteristics should be employed; and unless there be some logical basis in this treatment, the classification will be inconsequent and erroneous.

An organ may be considered with regard to any of the following characteristics: color, consistency, volume, shape, structure, differentiation of its parts, position with regard to other organs, and number. The guiding principles in determining which should be employed as the basis of treatment are two, the degree of conservatism of the characteristic and the degree in which the characteristic represents the organ as a whole. Judged in this way, the characteristics of *color* and *consistency* are found to be of small value. *Number* is in strict sense not a characteristic of an organ, but duplication of organs is a characteristic of the general plan, as in bilaterally symmetrical forms where certain organs are paired, in metameric forms where they are serially duplicated, in radiate forms where they are antimerically duplicated. Sometimes an organ is excessively duplicated without any corresponding duplication of the body plan (*e. g.*, testes within one proglottid of a Cestode). The relation that the number bears to the larger divisions of the organization must be determined, in order for us to conclude whether the two correspond; for when number of organs and number of larger body parts correspond, the number would have more significance for the comprehension of the whole organization than if there were no such correspondence. Number is a characteristic which must always be carefully considered, for the relative degrees of duplication of organs and of their concentration or concrescence are of great importance in estimating the affinity of the organism to its allies.

The *position* of an organ with regard to the other organs is also a characteristic to be carefully considered, though perhaps it has not the same value as number ; thus whether the central nervous system lies above or below the intestine or heart, and whether the skeleton is external or internal. For if variations in the position of an organ cannot be readily explained by change in mode of life, it is probably the case that more conservative intrinsic growth energies are the occasion, and the latter should be ascribed great importance until the contrary be proved. It is just these phenomena, which seem most inexplicable, that should serve as warning signals not to proceed further until many explanations for them have been tested. Why the genital orifices in certain Rhabdocœlida are near the anterior end, in others near the posterior end of the body, we do not yet understand, and it is very difficult to give a good reason for the shifting of such important structures. But until it is proved that the shifting is due to some trivial cause, we have no right to disregard in classification such differences of position. Again, such an apparently trivial characteristic as the position of the anus: in most freely motile Metazoa it is ventral, in the Entomostraca and the Rotatoria it is dorsal. The dorsal position in these two groups has been given no particular morphological importance, as far as I can recall; but without wishing to prejudice the question it may be asked, is this dorsal position to be explained simply as due to peculiarities in the external skeleton? If it cannot be so explained, then it is a characteristic which should receive more attention than it has heretofore. The proboscis of an *Echinorhynchus* is morphologically a part of the body wall, that of a Turbellarian a fold of the pharynx alone; this difference of position is sufficient to disassociate these structures, even though they should agree closely in anatomical details, and here, then, relative position would be of more value than structural detail of the organ itself. The relative position of internal organs, which are not immediately exposed to change in external environment, is a characteristic which must receive careful consideration.

The other characteristics of an organ, form and differentiation of its parts, are especially important. The general form is of more importance for phylogeny than its minute histological structure, and its grosser than its finer structure. This point has been well expressed by E. B. Wilson:[18] "The nephrostome is a nephrostome all the same whether it consist of one cell, two cells, or many cells. Its form and function are both independent of the number of component cells. Cells multiply, but the organ remains the same throughout. So far as homologies are concerned, the existence of cells may be ignored." And to consider the nephridia of Turbellaria, Nemertini and Annelida. The nephridia of the first two mentioned groups are rightly considered to be of essentially the same type and different from the nephridia of Annelida, since they consist of continuous longitudinal ducts with numerous lateral branches, while a nephridium of an Annelid is essentially a single, unbranched tube; we cannot say there is a sharp distinction between the nemertean and the turbellarian type, because the terminal end of a branch in the former is multicellular, in the latter unicellular. Similarly, in certain Nematoda the intestinal lumen is intercellular, in others intracellular; but this histological difference should not lead us to doubt the correspondence of these intestines. In regard to the nephridia of Nematoda, there is still reasonable doubt whether they should be considered comparable to the protonephridia of Turbellaria; but this doubt is based upon their general anatomy (lack of lateral branches), not upon the fact that in the one case they are unicellular and in the other multicellular. In other words, in considering the homologies of organs one should not look for cell nuclei. The grosser differentiations of an organ are of the first importance in phyletic classification. A compound eye of an Arachnid is essentially a single lens in conjunction with retinal cells arranged in retinulæ; and we characterize it so in comparison with the compound eyes of insects or crustaceans, and need not define it further in terms of finer structure of rhabdomes of nerve endings. The fingers on the hand of a urodele may be compared with those of a mammal, because of their essential similarity and corresponding relations to the fore-limb, though in the one the skeletal rays are cartilaginous and in the other osseous. The method should be in general exactly that by which an anatomist examines any part—first, a careful examination of the whole with the naked eye, then of a part with a low degree of magnification, then of smaller parts with greater magnification—but with this difference, that the more minute the examination becomes the less general value the parts have for the purposes of phylogeny.

---

[18] *The Embryological Criterion of Homology,* Woods Holl Lectures, 1896.

To summarize, all characteristics of an organ have value for the phylogenist, except the more superficial ones of color and consistency. Those characteristics which most completely represent the organ as a whole are the ones of most importance, and minute details of structure may lead to erroneous conclusions with regard to homologies. Degree of conservatism is also a criterion of the value of a characteristic. Broader homologies must be based upon the relations to the rest of the organization, and upon the grosser differentiations.

VII. Comparison of the Methods of Embryology and Comparative Anatomy in Determining Homologies.

The organism is to be classified at the end of its development, for reasons given in section III. But so far there has been no discussion as to whether for determining homologies the organism should be considered at this stage alone, or whether in previous stages also. The question is, is the determination of homologies to be made on the data of comparative anatomy or of comparative embryology, or upon both ? In other words, are homologies to be drawn from essential similarity of adult structure, or of development? As to which of these methods is the more correct, has been and probably will continue to be a question of dispute. The comparative anatomists maintain one side, the embryologists another; and probably because the former are less conversant with the facts of embryology, and the latter with the facts of adult structure. Those who are at the same time comparative anatomists and embryologists have in general taken more of a middle course.

The argument for the embryological method is mainly based upon the hypothesis that the ontogeny is a more or less true parallel to or repetition of the phylogeny. The strength of the embryological method depends mainly upon the strength of this hypothesis, so that we have first to examine its correctness. This is the basis of the embryological method in the study of phylogeny, and therefore in the search for homologies, using the term "homology" in the sense of "homophyly." Certain writers have been more cautious, considering homology to depend upon corresponding ontogenetic mode of development, whether the ontogenetic correspond to the phylogenetic or not. But in assuming that the ontogenetic development may not correspond to the phylogenetic, they have no basis for assuming that essential ontogenetic agreement denotes homology, if homology be used in the sense of homophyly.

(*a*) *Hypothesis of the Correspondence of Ontogeny and Phylogeny.*

It is not my purpose to give a historical sketch of this hypothesis and of the many opinions which have been expressed with regard to it, but merely to state briefly the tenets, and then to examine them critically for our present purpose.

This hypothesis is an old one, going back to the eighteenth century, if not indeed to the seventeenth, and as von Baer expresses it, is "mehr eine Entwickelungsstufe der Wissenschaft als das Eigenthum eines einzelnen Mannes." It was held in the early statement of it, that a higher form in its development passes successively through lower animal forms—*i. e.*, that the ontogeny is a relatively exact repetition of the phylogeny. The first logical criticism of the hypothesis thus stated was made by von Baer,[19] who postulated the following laws of the development of the individ-

---

[19] *Entwickslungsgeschichte der Thiere*, 1828.

ual: "(1) Dass das Gemeinsame einer grössern Thiergruppe sich früher im Embryo bildet, als das Besondere. (2) Aus dem Allgemeinsten der Formverhältnisse bildet sich das weniger Allgemeine und so fort, bis endlich das Specialiste auftritt. (3) Jeder Embryo einer bestimmten Thierform, anstatt die anderen bestimmten Formen zu durchlaufen, scheidet sich vielmehr von ihnen. (4) Im Grunde ist also nie der Embryo einer höhern Thierform einer anderen Thierform gleich, sondern nur seinem Embryo." He objects to the hypothesis that no adult animal has a yolk sack; that none is surrounded by embryonic fluids; that it is not the case that an embryo of a higher animal in each ontogenetic stage corresponds in every point with an adult individual of a lower species; that it is not the case that in the ontogeny of a lower form structural relations do not occur which are found in the adult of a higher form; and that parts which are characteristic of only the highest forms do not appear latest in the ontogeny. He recognizes that there are indeed many correspondences between ontogenetic stages of higher and adult stages of lower forms, but contends that it is " noch nicht erweisen, dass jeder Embryo einer höhern Thierform allmählig die niederen Thierformen durchläufe, vielmehr scheint sich der Typus jedes Thiers gleich anfangs im Embryo zu fixiren und die ganze Entwickelung zu beherrschen." Any one who reads carefully this classic work will find there stated, very acutely and logically, most of the objections, generally supposed to be of much more modern date, to the theory.

Fritz Müller[20] held that the theory is in the main correct, but pointed out that phylogenetic traces may become more or less obliterated in the ontogeny; he held, accordingly, that the lack of exact correspondence is due to embryos adapting themselves to new modes of life. Haeckel has developed the theory most thoroughly; and has consequently used it most in the determination of phylogenies. He terms the theory the " biogenetisches Grundgesetz," and states it: " Die Ontogenie (Keimesgeschichte) ist eine kurze Wiederholung der Phylogenie (Stammesgeschichte)." He also introduced the terms " palingenesis" and "cenogenesis," and states: "Die Phylogenesis ist die mechanische Ursache der Ontogenesis." Thus Haeckel's position in regard to this hypothesis is in some respects a return to the opinion that was dominant before the time of von Baer.

---

[20] *Für Darwin*, 1864.

Hatschek[21] gives a brief but able consideration of this hypothesis: " Die Ergebnisse der vergleichenden Ontogenie haben stets nur den Werth von Wahrscheinlichkeitsschlüssen, genau in demselben Grade wie die der vergleichenden Anatomie. Die relative Sicherheit hängt in beiden Fällen nur von der Menge der Praemissen und von der Schärfe des Schliessens ab. . . . . Die Methode der vergleichenden Ontogenie ist eine Erweiterung der vergleichend anatomischen Methode (Festellung von Homologie und Analogie) durch Anwendung derselben auf Formenreihen. . . . . Da der individuelle Organismus nicht durch einen einzigen Formzustand, sondern durch eine Formenreihe repräsentirt ist, die er während seines individuellen Lebens durchläuft, so kann es auch nicht genügen, allein die Endformen zu vergleichen, sondern es muss die ganze Formenreihe berücksichtigt werden." He concludes also that when a larval or embryonic form is characteristic for a large group, we are only justified in concluding that the ancestor of such a group possessed also this larval or embryonic form; and only when the latter shows great correspondence with the adult stages of lower forms can it be said with great probability to correspond to a similar ancestral form.

As the biogenetic law is generally held to-day, it assumes that the stages of the individual do not repeat but only to greater or lesser degree parallel the stages of the race: the correspondence is not one of repetition but of parallelism. And in each particular case the palingenesis must be distinguished from the cenogenesis. The possibility of error is in proportion to the difficulty of making this distinction.

(*b*) *On the Application of this Hypothesis.*

On the principle that the organization should be considered as a whole, there is no *à priori* reason for disregarding the various stages of the organization. With von Baer we may say that the individual development consists in a progress from the more general to the more special, and the further the individual of one race develops the more it diverges accordingly from individuals of other races. The biogenetic law is an assumption, and put into practice it may become a *circulus vitiosus;* but at the same time the main principle of comparative anatomy is also a postulate, namely, that essential agreement of adult structure denotes phyletic relationship. When the conclusions from the embryological basis do not agree with those from the anatomical, how is the decision to be made ?

---

[21] *Lehrbuch der Zoologie,* 1888.

In the first place, it is evident that the adult stages of organisms do represent phyletic stages, while in many cases ontogentic stages certainly do not. There can also be no doubt that the characters of the adult become " segregated " (Lankester) or " accelerated " (Cope) gradually further back into the ontogeny, as the racial progress continues, and so in the course of time would modify more and more the ontogeny as a record of the phylogeny. Also the sequence in the formation of the organs of the individual need not be the same as their sequence in the racial development; a point already made by von Baer, and to-day particularly insisted upon by Keibel and others.

In the second place, the individual must be classified at its mature stage in order to show its full degree of racial development. This principle, therefore, demands that the organization should be primarily considered at that stage. Judged from this point of view, any classification based entirely upon the mode of cleavage of the ovum or upon the occurrence of a certain kind of larva is incorrect, because it would represent the organism before it had reached its full specialization. Here come such classifications as that given by Friedrich Brauer for the Diptera (according to the position of the split in the shell of the pupa), and that which has led to the formation of the group of the Trochozoa.

Thirdly, we have to consider on what the correspondence of the ontogeny to the phylogeny rests. The facts of comparative anatomy show that the groups of the Annelida and Mollusca are phyletically connected. The careful studies of the cell lineage of types of these two groups have shown a surprising and wholly unexpected degree of correspondence in their mode of cleavage, up to the time of the appearance of the larval organs; while from another standpoint the larval types of both show close structural similarity. This is sufficient as a case for examination, though a number of others would suffice equally well. Now, does this correspondence of the ontogeny to the phylogeny depend upon the individual inheriting the successive preceding stages of the race, or upon the growth-energies of the race being essentially the sum total of the growth-energies of the individuals which compose it ? Evidently the latter, with the reservation that growth-energies are directed to the development of structure immediately in view, and with change of habit become correspondingly modified. If at a certain stage the individual is pelagic and later sessile, the growth-energies are first directed to the formation of the structures necessary for the habits of the pelagic period, later to the formation of those for the sessile condition. If the pelagic habit became lost, the growth-energies from the first become directed toward the development of structures essential for the sessile state.[22] There is here a continual adaptation to new conditions of life, restricted by the line of direction held by these energies in preceding ontogenies, the restriction more or less directly diminishing according as the preceding ontogeny is far removed, and according to the degree of plasticity of the organization.

Obviously, in regard to the Annelida and Mollusca, we may conclude either that their cell lineage is so closely correspondent because of their close genetic affinity (there not having been time for a great difference to arise), or because the cell lineage in both is followed by a more or less similar larval stage. In the former view genetic affinity is postulated, in the latter convergence of cleavage on account of the similarity in the larvæ. As to the larvæ, these may be alike because of the genetic affinity of the two groups, or because they lead a corresponding mode of life and are formed at an equally early period. At every point in this discussion of embryonic and larval homologies we find the possibility of two divergent opinions. The *pros* and *cons* of the two positions have been more or less fully discussed by the cell lineagists, and it is not for me to enter into questions concerning the homologies of blastomeres. It is sufficient to state here that the cell lineagists have more or less divided opinions on these points, as can be seen by an examination of the papers of E. B. Wilson (different opinions expressed in successive studies), Conklin, Mead, Treadwell, Lillie, Eisig, Heath, and others.

One point may be made here. If the biogenetic hypothesis is true, then in general the earlier the stage of the ontogeny the broader should be the homologies to be determined from it. But this not only does not accord with the facts (as in the case of embryonic structures which could not have been represented in any adult form), but would lead to the absurdity of homologizing all ova –an absurdity because the egg of a mammal is as much a mammal as the adult, and the egg of an arachnid equally well an arachnid. Ova of different organisms are more or less alike, because they all represent single cells with generalized potentialities, and hence usually not great structural differentiations; and not because they represent a repetition of a protozoan ancestor. Sexual reproduction, as clearly shown by Richard Hertwig, is characterized as reproduction by means of germ cells, whether the germ cell be fertilized or not (parthenogenesis); and since sexual reproduction is found in all Metazöa, the beginning of each metazoan individual is a single cell (or a union of two cells).[23] And the gradual ontogenetic differentiation of the organism being accompanied by cell division, each metazoan must have a two-cell, a four-cell stage, etc.; in the course of the further differentiation these must become arranged into layers, and there must be folding of these layers. Thus agreement in the early ontogeny at least is directly referable to reproduction by means of germ cells, and to the development of these cells proceeding by division; this is the immediate explanation, and much more circuitous is the theory that in the phylogeny there followed upon the unicellular condition a parvicellular, and upon that a multicellular. Thus the earliest of the processes of the ontogeny, which on the assumption of the biogenetic theory should show the broadest homologies, are the very ones which show homologies least clearly. The ovum of a mammal is a mammal and not a protozoan; and there is no adult protozoan known which is structurally similar to the ovum of any known metazoan. In most cases the cytoplasmic differentiation of a protozoan is much greater than that of an ovum of a metazoan, yet the metazoan is higher in the phyletic scale.

---

[22] This is necessarily not an exact statement of the facts. Exactly stated, the growth-energies are *immediately* directed to the establishment of the next following stage. Yet, certainly all the energies are directed toward the establishment of the ultimate structural condition.

Thus the organism represents in its ontogeny merely conditions preparatory and subservient to the perfected, terminal stage. The structural conditions of this stage control, more especially where the ontogeny is without metamorphosis, the nature of the conditions that precede it. Metamorphosis and larval conditions have probably been secondarily acquired, and direct development is the more primitive; for metamorphosis is a result of change of habit at different periods, and such change of habit is not as primitive as a habit continuous through the life of the individual, since it is more complex. It will, of course, be understood that in the case of certain phyla, such as the Annelida, I grant that the larval type of development may be primitive, and that forms which do not show it have lost it; but that it could not have been primitive for the ancestors of the Annelida. There is also good reason to conclude that the larvæ of different phyla of organisms may be alike, because they are ontogenetic forms of essentially the same mode of life, and because their organs are comparatively few in number and at an early stage of specialization. The earlier the stage of the ontogeny, the greater in general should be the agreements in structure, not because the homologies are more comprehensive at that time, but because there are fewer structural parts to show differences.

---

[23] Of course in the case of a protozoan the single cell is at once soma and germ plasm, and is not to be compared to the germ cell alone of Metazoa.

Thus far we have criticised the application of the biogenetic theory to the determination of homology. These criticisms might be multiplied and examined more in detail; and they are objections which have been made before, though not from the standpoint of the necessity of classifying the organism at its terminal stage.

Now we have to consider in what respects the study of ontogenetic conditions is necessary in the search for homologies. Homology is a likeness of descent, is homophyly, whether it be based upon adult or embryonic structure, provided that there is a good basis employed in its determination. It is an erroneous position to hold that the adult anatomy alone is sufficient for determining all homologies; it is equally erroneous to hold that homologies can be determined on the basis of similarity in ontogenetic formation alone. Whenever a structure is greatly degenerate in the adult condition, a study of its preceding ontogenetic stages is often the only guide we have as to its homologies.[24] Then in organisms which are isolated at the present time, whose more immediate relatives have become extinct, it is particularly necessary to know the organization at all its periods.

---

[24] Often, however, a highly degenerate structure can be explained by comparative anatomy as well as by embryology. Thus the pineal gland of a bird and the pineal eye of certain reptiles.

In conclusion, we have to bear in mind that of first importance in classification is the terminal, perfected stage of the organism, since this ontogenetic stage is also an actual phylogenetic stage. The further removed from this stage the further from actual phyletic conditions, and therefore the greater chance of error in interpretation. The correspondences between the ontogeny and the phylogeny are not repetitions but parallels, and in many cases parallels that are so imperfect that it is always necessary to decide what is palingenetic and what cenogenetic. The decision in regard to this point is necessarily more arbitrary and subjective than a decision upon similarities of adult structure; for the embryological method, in addition to assuming in common with comparative anatomy that essential similarity of structure and position denotes homology, has also to assume as correct that the course of the ontogeny is more or less similar to that of the phylogeny. Comparative anatomy is not obliged to make this assumption, and so has one premise less. In this conclusion we do not diminish the value of comparative embryology, but only restrict the application of its facts. Comparative embryology has been fully as productive as comparative anatomy in establishing working hypotheses, the value of which for research is indisputable. But it is, in the main, from comparative anatomy that the phylogeny is to be determined; and from comparative embryology an understanding of the growth-energies, and therefore a more complete comprehension of the adult structures. And it is the logical method to investigate all the series of forms of the organism, so as to reach the most comprehensive concept of the organization as a whole.